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# Enhanced brainstem and cortical encoding of sound during synchronized movement

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ABSTRACT

Movement to a steady beat has been widely studied as a model of alignment of motor outputs on sensory inputs. However, how the encoding of sensory inputs is shaped during synchronized movements along the sensory pathway remains unknown. To investigate this, we simultaneously recorded brainstem and cortical electro-encephalographic activity while participants listened to periodic amplitude-modulated tones. Participants listened either without moving or while tapping in sync on every second beat. Cortical responses were identified at the envelope modulation rate (beat frequency), whereas brainstem responses were identified at the partials frequencies of the chord and at their modulation by the beat frequency (sidebands). During sensorimotor synchronization, cortical responses at beat frequency were larger than during passive listening. Importantly, brainstem responses were also enhanced, with a selective amplification of the sidebands, in particular at the lower-pitched tone of the chord, and no significant correlation with electromyographic measures at tapping frequency. These findings provide first evidence for an online gain in the cortical and subcortical encoding of sounds during synchronized movement, selective to behavior-relevant sound features. Moreover, the frequency-tagging method to isolate concurrent brainstem and cortical activities even during actual movements appears promising to reveal coordinated processes along the human auditory pathway.



## 1. Introduction

Movement synchronization to a steady beat is a fundamental sensorimotor skill, which has been extensively studied as a model of tight temporal alignment of motor outputs to sensory inputs (Repp, 2005; Repp and Su, 2006–2012). Most of the studies have focused on the neural correlates of the motor output (see, e.g., Gerloff et al., 1998; Penhune et al., 1998; Jäncke et al., 2000; Ullén et al., 2008; Bengtsson et al., 2009; Ullén et al., 2008). However, little is known about the impact of motor outputs on the processing of sensory inputs on which the movement is synchronized. Recent models of active sensing have proposed that the motor system could modulate the cortical processing of sensory information. This modulation would optimize the coordination of motor output on sensory inputs over time through cyclic fluctuations in sensory gain related to motor acts (Morillon et al., 2014; Schubotz, 2007; Schroeder et al., 2010; Zagha et al., 2013). This dynamic sensory gain could act as a filter, sharpening the temporal representation of auditory inputs, thus facilitating perception of behavior-relevant items (e.g. temporal structure of a dynamic sensory input to which a movement needs to be aligned in a sensorimotor task) (see e.g. Morillon et al., 2014).

Importantly, this online modulation of the sensory input may arise earlier in the auditory hierarchy, namely at brainstem level of the sound encoding. Indeed, a specific link between sensorimotor synchronization behavior and brainstem auditory processing has been highlighted in previous work (Tierney and Kraus, 2013, 2014). For example, it has been shown that the variability in tapping on a steady beat correlates with the variability in response latency in the auditory brainstem (Tierney and Kraus, 2013). Moreover, to account for the fast corrections usually observed in tapping movements synchronized to sound onsets (phase corrections <100 ms of latency in finger tapping on sound sequences; see e.g. Hove et al., 2014b), recent work has suggested the existence of a rapid subcortical pathway involved in movement correction (Schwartze and Korz, 2013; Hove et al., 2014a; Doumas et al., 2005; Bijsterbosch et al., 2010). Specifically, a rapid subcortical/cerebellar pathway (via the brainstem's dorsal cochlear nucleus) may be responsible for the highly accurate encoding of sound

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onsets timing and the fast transmission of the temporal structure of sounds (i.e. the sound envelope) to thalamic and cortical targets (Schwartze and Korz, 2013). This rapid feedforward route with highly accurate temporal precision, modulated itself via corticofugal fibers in a continuous feedforward-feedback dynamic, could be critical in sensorimotor synchronization (Schwartze and Korz, 2013), thus placing the brainstem auditory nuclei in a key role in monitoring sensorimotor temporal alignment. However, there is currently no direct evidence of the modulation of the auditory brainstem response when synchronizing movements to sounds.

The general goal of our study was to fill this gap in knowledge by directly testing whether cortical but also brainstem responses to sound are shaped during synchronized movement to the sound. Previous work has provided evidence that brainstem auditory processing can be dynamically modulated by task contexts in humans (Galbraith et al., 1998; Rinne et al., 2008; Chandrasekaran et al., 2009; Lehmann and Schönwiesner, 2014) and also non-human animals (Slee and David, 2015). This sensitivity to ongoing contextual and task demands has been explained by the existence of efferent connections from the cortex to subcortical nuclei (see e.g. Winer, 2006; Winer and Lee, 2007; Bajo and King, 2013). These efferent corticofugal fibers project to the major levels of the auditory system, including the thalamus, the inferior colliculus, the superior olivary complex and the cochlear nucleus, allowing the brainstem encoding of sounds to be modulated depending on the level of activity in cortical auditory areas (Diamond et al., 1969; Weedman and Ryugo, 1996; Winer et al., 1998; Mulders and Robertson, 2000).

Building on this work, the current study aimed to test a more specific hypothesis, — i.e. that the brainstem encoding of sound would be enhanced during auditory-motor synchronization. More specifically, we hypothesized that this sensory gain would be selective to the sound envelope, as this sound component drives the movement synchronization, in contrast with the tones' pitch which is a sound component not directly relevant to the tapping behavior. Hence, we aimed to test whether the envelope representation at brainstem level was enhanced *during* synchronized movements, thus providing first evidence of auditory brainstem modulation driven by a task involving sensorimotor temporal alignment. Alternative to this sensory gain hypothesis however, one could predict to observe a sensory attenuation, due to an effect of agency related to the synchronization between sound and tapping (Schröger et al., 2015; Timm et al., 2014).

Processes of sensory modulation throughout the human auditory pathway remain poorly understood, probably due to the scarcity of methods to simultaneously measure the activity at different levels of the auditory pathway with high temporal resolution, specifically while performing movements. The current study addressed this question by investigating concurrent activities produced by distant neural populations throughout the auditory hierarchy. Participants listened to a chord made of three tones periodically amplitude-modulated in order to induce a steady beat. They were asked to carefully listen either without moving or to tap in synchrony to every second beat. Importantly, our study made an original use of the frequency-tagging method to simultaneously measure cortical and brainstem responses to sounds with electroencephalography (EEG). The frequency-tagging method consists in identifying and isolating different components of the neural response to a stimulus based on the expected frequencies of these components (i.e. steady-state evoked potentials, or SS-EPs; see e.g. Galambos et al., 1981; Rees et al., 1986; Picton et al., 1987; Regan, 1989; Ross et al., 2000, 2004; Bidet-Caulet et al., 2007; Norcia et al., 2015). In the current study, these frequencies were determined by the frequency structure of the stimulus itself (i.e. sound envelope at 2.4 Hz and harmonics, partials at 200, 400 and 600 Hz and sidebands at partial frequencies $\pm$2.4 Hz and harmonics). Importantly, the frequency content of the sound was specifically set such as to elicit frequency-locked responses that are likely to originate in most part from the brainstem auditory nuclei (i.e. partials and sidebands >200 Hz) and the cortex (i.e. amplitude modulation <3 Hz) respectively (Skoe and Kraus, 2010a). Hence, the frequency-tagging approach appears to be particularly well suited to isolate concurrent cortical and brainstem processes.

We also moved the method a step further by capturing these activities not merely during perception but also during actual movements synchronized on the dynamic sensory input, thus providing first empirical cues about the possible effects related to auditory-motor coordination on the subcortical encoding of sound. Moreover, a significant signal-to-noise ratio was expected for both brainstem and cortical activities, although the auditory stimulation lasted <7 min in total per condition. Indeed, the use of long-lasting continuous stimuli allowed a fine spectral resolution (0.02 Hz) to be obtained in the current study, thus concentrating the frequency-locked activities within very narrow frequency bands in the EEG spectrum (Norcia et al., 2015). In addition, the use of long-lasting sequences of continuous stimuli were likely to improve the opportunity to capture dynamic aspects of the processes at stake in sensorimotor synchronization, in contrast with transient event-related potentials (ERPs) reflecting transient neural responses triggered by the occurrence of transient stimuli (Norcia et al., 2015; Nozaradan, 2014).

## 2. Materials and methods

### 2.1. Participants

Twenty-two healthy volunteers (10 females, 12 males, all right-handed, mean age 21.2 $\pm$ 2.9 years, aged between 18 and 29) took part in the study after providing written informed consent. They were either music amateurs as listeners or dancers, or considered as musicians according to the number of years of music practice (11 participants with 8.5 $\pm$ 3.8 years). None had prior experience with the tapping task used in the present study. They had no history of hearing, neurological or psychiatric disorder, and were not taking any drug at the time of the experiment. The study was approved by the Research Ethics Committee of the Faculty for Arts and Sciences of the University of Montreal.

### 2.2. Auditory stimulation

The auditory stimulus consisted in a continuous sequence of 39.5 s. The sound was composed of a harmonic tone with three partials at 200, 400, and 600 Hz composing a consonant chord (Fig. 1). These frequencies were chosen because frequency-following (i.e. frequency-locked) responses at these rates recorded in humans with scalp EEG are most likely to originate from brainstem nuclei of the ascending auditory pathway due to the low-pass limitation in the production of sustained frequency-locked responses to sounds in the human auditory cortex (Skoe and Kraus, 2010a). A harmonic relationship between the three tones was chosen to optimize the emergence of brainstem frequency-following responses to the chord, as brainstem responses to consonant intervals are known to be more robust than for nonharmonic intervals (Bidelman, 2013). A beat was induced by modulating the amplitude of the chord at a frequency of 2.4 Hz (144 beats per minute), using an asymmetrical Hanning envelope (12 ms rise time and 404 ms fall time with a modulation depth of 75%, as in Nozaradan et al., 2015). A 2.4 Hz frequency was chosen because (i) this tempo lies within the ecological range of beat perception and production (Drake and Botte, 1993), (ii) we previously showed that this beat frequency elicits a measurable steady-state evoked potential (SS-EP) in the human EEG (Nozaradan et al., 2011, 2015), (iii) pilot experiments showed that participants are comfortable tapping on every second beat at this beat frequency, and (iv) frequency-locked responses to amplitude modulation of a carrier tone below 20 Hz are most likely to originate from cortical auditory sources rather than brainstem nuclei when recorded with scalp EEG (Wong and Stapells, 2004; Ross et al., 2000). An